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DEVELOPMENT OF PLUTEUS ADMIRABILIS AND TUBARIA FURFURACEA[1]

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(WITH PLATES I–V AND EIGHT FIGURES)

Since there is no published account of the development of any species of *Pluteus* or *Tubaria*, it seemed desirable to the writer to study representatives of these genera. Especially was this true for *Pluteus*, because in observing young stages it was difficult to determine whether the hymenophore was endogenous or exogenous in origin. The prominent cystidia, also, and the unusual structure of the trama of the gills, the filaments composing it consisting of "long cylindrical cells converging as they descend in the gills and often lying more or less crisscross at different angles of divergence," as mentioned by ATKINSON (2) in his description of *Leptonia seticeps*,[2] offered an interesting field for investigation. ATKINSON has found this structure of the trama to be characteristic of all species of *Pluteus* and *Volvaria* examined by him.

While the various species of *Pluteus* are abundant in most regions, the fruit bodies are usually formed singly or with only a

[1] Contributions from the Department of Botany, University of Nebraska, New Series, No. 27.

[2] *Leptonia seticeps* Atk. (Jour. Myc. 8:116. 1902) = *Pluteus seticeps* Atk. MSS. ATKINSON came to consider this form a true *Pluteus*. At the time he described it he placed it in *Leptonia* because of the slight attachment of the gills to the stem. His extensive studies on the structure of the *Agaricaceae* have shown that structurally it agrees in all ways with *Pluteus* and not with *Leptonia*.

AUG 7 - 1923

few closely associated. This habit makes the collection of material for developmental study very difficult. *Pluteus admirabilis* Peck occurs in troops more commonly than most other species, and its bright yellow color makes the young basidiocarps quite easily distinguishable. I began my collection of this species while in the Adirondacks on a collecting trip during July 1916. A large part of the material was collected from troops where only 3 or 4 basidiocarps of suitable age were obtainable. The largest individual collection was secured after my return to Ithaca, in the Van Samtford woods near Freeville, New York, during the latter part of August 1916.

The material for the study of *Tubaria furfuracea* Gill was collected in Cascadilla ravine, and along the banks of Fall Creek, on the Cornell University campus, during the early summer of 1916, where the plants were growing very abundantly on the leaf mold and loam in a small wood. The plants occurred in troops upon an abundant mycelium which permeated the substratum. All stages in development were to be found upon this mycelium when the fruits first began to appear.

The material for the study of both genera was fixed in chromacetic and Benda's fluids, cleared in cedar oil, and imbedded and sectioned in paraffin.

Pluteus admirabilis

ORIGIN OF HYMENOPHORE

No fruit body was obtained before the beginning of any differentiation had taken place in the primordium of the basidiocarp. The youngest stage secured (fig. 1) was a little over 0.5 mm. in height and already showed a differentiation into primordia of stipe, pileus, and hymenophore. The primordium of the stipe is made up of loosely interwoven, much branched filaments, uniformly about 3 μ in diameter, which become less interwoven and show many free ends near the surface, as can be seen in fig. 29, a higher magnification of the same fruit body. This tissue gradually passes into that of the primordium of the pileus, which at the base has the same structure as the primordium of the stipe, but soon opens out into a less interwoven tissue in which the filaments lie almost parallel to each other and radiate in a fanlike manner, with free

ends on the surface. These filaments are slightly larger than those of the stipe, often reaching 4 μ in diameter at their ends. This divergent growth of the hyphae making up the primordium of the pileus is similar to that described by De Bary (12, 13, 14) for *Nyctalis asterophora*, *N. parasitica*, and *Collybia dryophila*, and by Blizzard (11) for *Omphalia chrysophylla*, *Clitocybe adirondackensis*, *C. cerussata*, and *Clitopilus noveboracensis*. The primordium of the hymenophore (fig. 29) consists of only a slight modification of these outward turning filaments such as cover the pileus and stipe. They

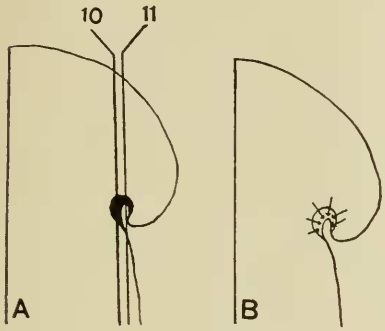

Fig. 1

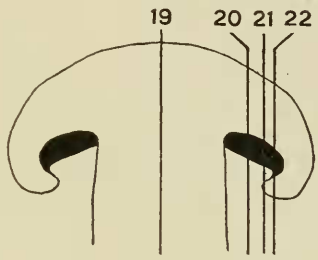

Fig. 2

Figs. 1, 2.—Fig. 1, *A*, diagram showing plane of sections shown in figs. 9–11; *B*, small arrows showing direction of growth in hymenophore of same basidiocarp; fig. 2, diagram of plane of sections shown in figs. 19–22.

are more closely packed together, smaller, and with slightly denser protoplasmic content.

Figs. 2–8 show median and tangential longitudinal sections of young basidiocarps in successive stages of development. In the fruit body shown in figs. 2 and 3, and more highly magnified in figs. 30 and 31, a definite palisade layer has been formed, and the loosely interwoven outer portion of the stem is more pronounced; otherwise the structures show no further differentiation. As growth progresses the margin of the pileus shows a strongly epinastic development, so that as the pileus enlarges the margin turns abruptly downward (figs. 4, 6), while the hymenophore still remains in the palisade condition, as shown by figs. 5 and 7. The continuation of this epinastic development causes the margin of the pileus

to roll inward so closely that the edge of the pileus becomes pressed against the loosely interwoven ends of the filaments covering the stem. Figs. 8 and 32 show a fruit in this condition with the ends of the filaments of the pileus and those of the stem intermingled. It is this condition that caused the uncertainty in the examination of young forms as to whether the hymenophore was endogenous or exogenous in origin.

The development just described reminds one of HARTIG'S (16) description of the development of *Armillaria mellea*. He found that the hymenophore developed exogenously at first, and that later by epinastic growth the margin of the pileus became incurved, and that the marginal veil developed from the interweaving of filaments growing from the margin of the pileus with similar ones growing out from the stem. This course of development, however, has been shown by BEER (10) and ATKINSON (5) not to be correct for *Armillaria mellea*. BLIZZARD (11) in his studies on exogenous forms found the pileus in several to be strongly incurved, but he did not report an interlacing of filaments from the pileus and stipe. At this stage of development the strong epinastic development ceases and the expansion of the pileus takes place more uniformly in all directions (figs. 9, 12, 15, 19, 23).

During the changes in the form of the pileus just described the general relations of hymenophore to stipe and pileus remain the same as seen in the younger stages (figs. 29, 30), but the palisade layer becomes more and more arched (fig. 32). The space between the arched hymenophore is lined with the uniform terete ends of the filaments of which the palisade layer is composed.

ORIGIN AND EARLY DEVELOPMENT OF LAMELLAE

Figs. 9–11 show low magnification of median and tangential longitudinal sections of a young fruit body in which the first trace of gill development is distinguishable. The location of these sections is shown in text fig. 1*A*, while the small arrows in text fig. 1*B* show the direction of growth in the hymenophore at this time. The gill salients arise as folds occurring in the angle between the stem and pileus where the palisade layer is first developed. The stem is narrower in the region of the developing hymenophore than below

it, so that in the tangential longitudinal section shown in fig. 10, and more highly magnified in fig. 35, the gills appear to extend as strands from pileus to stipe. The direction of the growth of the hymenophore, however, as shown in text fig. 1*B*, continues to be the same as in the level palisade condition (figs. 30, 32), so that the cells making up the fundament of the trama (fig. 35) are transverse sections of filaments extending outward at right angles to the plane of the sections. The hyphae making up the subhymenium and the fundament of the trama are smaller than in the young palisade condition.

Figs. 12–14 show a slightly older but somewhat depauperate basidiocarp in median and tangential longitudinal section. Here the young gill salients whose development is centrifugal are clearly shown. Figs. 33 and 34 show the detail of this specimen. The depauperate condition of the fruit is shown by the scanty protoplasmic content and by the enlargement of the cells to a condition characteristic of older fruits. The development having been stopped at this age, the relation of the parts would probably remain identical with those of the normally developing basidiocarps. That this would be the case is substantiated by the observation of other depauperate fruits sectioned, in which development had been arrested at all stages.

Because of the strong incurving of the margin of the pileus after the beginning of gill development, and as the expansion of the fruit body progresses along with gill development, the palisade layer constantly present toward the margin of the pileus is always on the interior (morphological under-side) of the pileus margin as seen in tangential section (figs. 15–18). In fig. 18, and better in a higher magnification (fig. 36), the palisade layer is thus shown. In figs. 19–22 a slightly older fruit body is shown, in which the hymenophore shows gills in the young salient stage on the incurved portion of the pileus. Fig. 37 is a higher magnification of the section shown in fig. 22. In this fruit body the gills are so broad that the tangential sections show the gills attached above and below, but in each case attached to the morphological under-side of the pileus, their point of origin. Text fig. 2 shows how the sections in this series were cut, and that the attachment of these gills above and below is due to the incurved form of the pileus.

The secondary gills originate at varying distances from the stem in the same manner as the primary gills, and their development progresses outward. Young secondary gills are shown in figs. 20, 22, 37, and 38. They are also well shown in a transection of the fruit body (figs. 24, 39). The primary gills during their origin and development are attached to the stem (figs. 9, 15, 30, 32), and in a transverse section of a fruit body (fig. 24), but they become free during the general expansion of the fruit body (fig. 23). In *Agaricus rodmani* ATKINSON (7) found that the gills were often attached to the stem in the early stages of development.

ORIGIN OF CYSTIDIA

During the origin of the gill salients the cystidia begin to appear (figs. 34–36). Text fig. 3 shows in outline the position of cystidia and basidia in the basidiocarp shown in fig. 36 as accurately as could be determined. As shown here, the filaments bearing both cystidia and young basidia pass out from the trama in a usually unbranched condition, the cystidia being only distinguishable from the basidia by their more scanty protoplasmic content and larger size. As the gills develop, however, the filaments leading out to the cystidia become enlarged and for some time remain little, if at all, branched, while those bearing basidia and paraphyses are smaller and much branched (figs. 38, 47, 47*a*, text fig. 4). *A* and *B* of text fig. 4 show the details of the gills at this stage as definitely as could be determined, *A* being a reconstruction of the portion shown in fig. 47*a*. A slightly older gill is shown in fig. 48 and text fig. 5, *A* showing the detail of the cystidium shown in fig. 48, and *B*, *C*, *D*, *E*, and *F* showing parts of other gills in the same series. The filaments bearing the cystidia seemingly branch somewhat during the later development and give rise to basidia and paraphyses, but even with the highest powers of the microscope it was difficult to determine positively. Cystidia

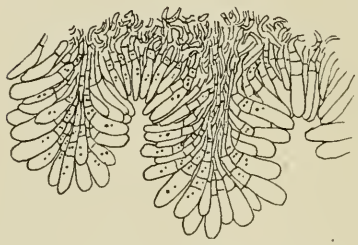

FIG. 3.—Course of filaments forming trama and leading out to young basidia and cystidia.

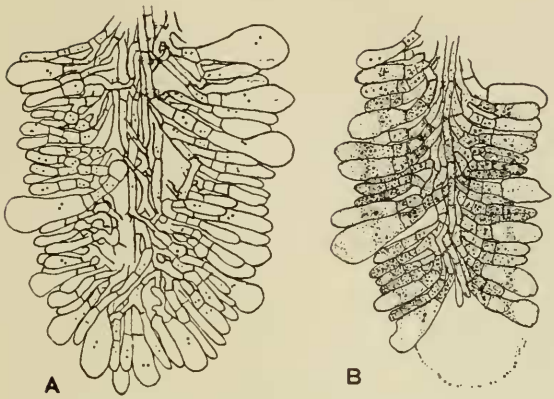

FIG. 4.—Structure of trama and origin of cystidia and basidia: *A*, reconstruction, made by aid of microscope, of photomicrograph shown in fig. 47*a*; *B*, another gill from same series outlined with camera lucida.

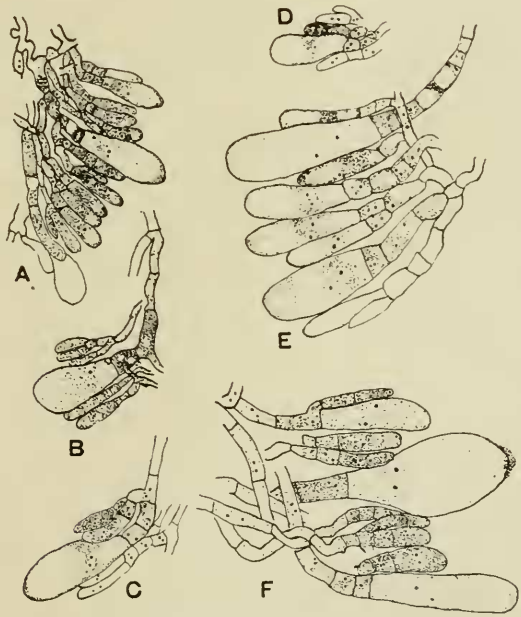

FIG. 5.—Origin of cystidia and basidia as seen in slightly older basidiocarp than that of text fig. 4: *A*, reconstruction of part of photomicrograph shown in fig. 48, made by aid of microscope; outlines of other drawings made with camera lucida.

and basidia in practically mature condition are shown in figs. 45, 46, 49, and in text fig. 6. The young basidia and cystidia, and the filaments which bear them, are constantly binucleate, as are the other cells of the young hymenophore, and in fact all parts of the young basidiocarp. The nuclei in the cystidia never fuse, and older cystidia lose their nuclei by degeneration. The cystidia are at all times much vacuolate and with scanty cytoplasm, while the basidia and paraphyses are filled with dense protoplasm. Very commonly the mature cystidium has a mucous cap (fig. 49), thus suggesting a possible excretory function, but this is not a constant characteristic.

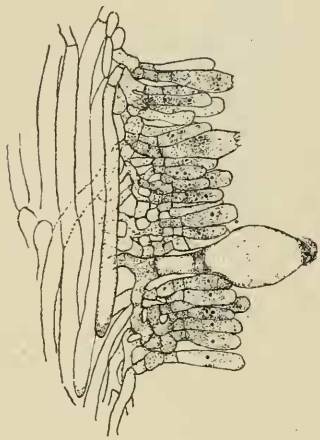

FIG. 6.—Detail of portion of gill shown in figs. 46 and 49, showing cystidia, basidia, paraphyses, and ultimate development of downward outgrowths from subhymenium (internal cystidia).

SURFACE CHARACTERS

As was noted in the description of the youngest stages of the fruit body, the outer portion of the pileus is made up of hyphae which radiate in a fanlike manner. As the development proceeds these hyphae become closely compacted (figs. 32; 33), but for some time retain this definite arrangement. The outer cells of this layer soon enlarge and appear as a uniform palisade layer, as shown in fig. 40, which is a higher magnification of the surface of the fruit body shown in fig. 19. The filaments making up the interior of the pileus branch and become much interwoven. As the pileus expands the cells forming the uniform palisade layer enlarge, giving the characteristic structure to the surface of the mature pileus (fig. 41). Structurally these cells are binucleate, and in origin seem to be homologous to the cystidia on the surface of the gills. These cells, even from youngest stages, are filled with a yellow granular content, however, and give to the pileus its characteristic color.

CHANGES TAKING PLACE IN TRAMA DURING DEVELOPMENT

As can be seen in figs. 36–38, 47, 48, and text figs. 3 and 4, the trama of the young gills is composed of slender, somewhat parallel filaments which are scarcely 2 μ in diameter at first, but soon become 2–2.5 μ in diameter, as seen in fig. 38. The trama of the gills is also very narrow and made up of relatively few filaments. As expansion of the fruit body takes place rapid changes occur in the trama. Fig. 25 is a transection of the gills of the plant shown in median section in fig. 23, where expansion is just well begun. A higher magnification of a part of these gills is shown in fig. 42. Here one observes a great multiplication of the filaments making up the trama, along with an enlargement of the individual cells. The multiplication of cells takes place largely in the region just below the hymenium, and is in the form of outgrowths of the subhymenial cells. These outgrowths extend downward and toward the center of the trama, as can be seen opposite *A* on the left of fig. 42, and in text fig. 7, which shows in a slightly diagrammatic manner the detail of this part of the section.

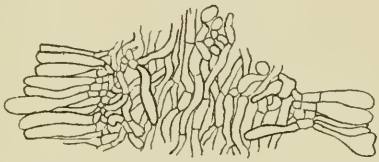

FIG. 7.—Portion of gill seen opposite *A* in fig. 42, showing beginnings of downward outgrowths from subhymenium which develop during expansion of basidiocarp.

These outgrowths continue their growth, maintaining a downward and inward direction, as is seen in a slightly older fruit body (figs. 26, 43), in which many of these filaments have reached the center of the trama. In these cells the protoplasm is much more dense in the apical end, and in many cases largely confined to this part. Figs. 27 and 44 show a still more extensive development of these filaments which have now become 4–5 μ in diameter, while figs. 28 and 45 show the gills when basidia have reached a 4-nucleate stage, but before spore formation, with the tramal cells about 7 μ in diameter. At this stage these cells are so long and thin-walled that some shrinkage takes place in all fixed material. Figs. 46 and 49 show, just below the base of the cystidium on the left, one of these filaments in good condition. This can be seen more clearly in text fig. 6. Fig. 50 shows the

trama of *Pluteus seticeps* Atk. MSS (see footnote 1), made from a freehand section which shows the typical structure of the trama of mature plants having this type of trama. The details of this can be seen more clearly in text fig. 8, which is a reconstruction from two photographs taken at slightly different foci.

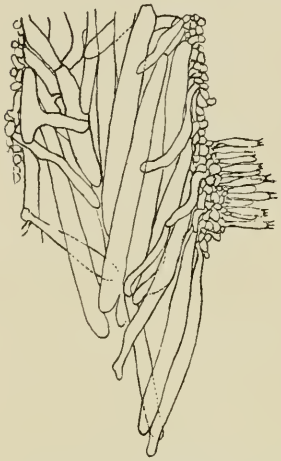

FIG. 8.—Culmination of downward outgrowths from subhymenium as seen in *Pluteus seticeps;* outlines obtained from combination of 2 photomicrographs made at slightly different focus on freehand section.

The cells composing the original trama in this species, and many other species examined, enlarge to the same size as those of the converging filaments arising in the subhymenium. This may not be true, however, of all species of *Pluteus*. In some specimens of *Pluteus longistriatus* the cells of the original trama seem to have entirely escaped the general expansion and remain slender, even in the mature pileus.

These downward growing filaments, originating as they do in the subhymenium, the same region from which the cystidia originate, and having the same general characteristics as cystidia (enlarged cells with scanty protoplasmic content), seem to represent a type of internal cystidium development. In some species of *Pluteus* a necklike constriction occurs near the apex of the external cystidium, and also on these internal outgrowths. These internal cystidia are at first binucleate, the 2 nuclei occupying a central position, as in the other cystidia, but the nuclei degenerate before the cystidia have attained the length shown in text fig. 6.

Tubaria furfuracea

EARLY DIFFERENTIATION OF PRIMORDIUM OF BASIDIOCARP

A median longitudinal section of an undifferentiated primordium of a basidiocarp is shown in figs. 51 and 78, the latter being a higher magnification of the upper portion of the former. It consists of

loosely interwoven hyphae about 2–3 μ in diameter, the external ones having firmer walls and taking the stain slightly more than those toward the interior. The fruit body illustrated in fig. 53 is smaller but shows some differentiation. There is a superficial zone made up of very loosely interwoven hyphae with firm walls. This region marks the beginning of a universal veil or blematogen layer, as this type of veil has been distinguished by ATKINSON (6). The filaments in this region show very little change in form or structure from those covering the outer portion of the primordium of the basidiocarp. Within this region is one of slightly smaller filaments with thinner walls and richer protoplasmic contents, merging into a less deeply staining region which has undergone no further differentiation. This interior zone of smaller, actively growing filaments marks the primordium of the stipe, which at this stage is somewhat conical in shape. Fig. 52 shows a somewhat older fruit body in which internal differentiation has been carried much farther. Here can be seen quite well defined the primordium of the stipe as an elongation of the conical region first differentiated, and the beginnings of the primordium of the pileus in a very slight enlargement of the apex of the stipe. The hyphae making up the densely staining region marking the primordia of stipe and pileus are smaller, about 1.5 μ in diameter, and much more closely interwoven than those of the outer portion, as can be seen in fig. 79, a higher magnification of a part of the fruit body shown in fig. 52. The blematogen and the filaments in the interior show the same characters as those of the young fruit body previously described, except that in the stipe the central filaments have come to lie somewhat parallel to each other, extending in a vertical direction. Figs. 54 and 55 show a smaller but older fruit body. The blematogen, stipe, and pileus are very clearly differentiated. As can be seen in fig. 80, a higher magnification of fig. 54, the filaments of the pileus are very compactly interwoven toward the interior, but become more and more loosely interwoven toward the margin, where they merge into the blematogen.

It is interesting to note that the stipe is usually the first region to be differentiated in several other endogenous forms, as in *Lepiota cristata* and *L. seminuda* (9), in several species of *Cortinarius* (15,

18), *Pholiota* (17), and *Hypholoma* (1). In all of these forms the differentiation of the pileus takes place in very much the same manner.

ORIGIN OF HYMENOPHORE AND ANNULAR PRELAMELLAR CHAMBER

The first trace of the origin of the hymenophore can be seen in the median longitudinal section of the basidiocarp shown in figs. 54 and 80, where the under surface of the pileus seems to take the stain more deeply. In this region the filaments are more slender, with dense protoplasmic contents, and lie more or less parallel to each other, thus marking the primordium of the hymenophore. Just below this there is a spreading of the filaments in the still undifferentiated ground tissue lying between the primordia of hymenophore and stipe, due to the rapid growth in the primordial parts. This can also be seen in the tangential longitudinal section of the same fruit body (fig. 55), which was taken midway between the stipe and the margin of the pileus. Figs. 56 and 57 are median and tangential longitudinal sections of an older basidiocarp, the tangential section representing the condition just beyond the stem. Higher magnifications of the same sections are shown in figs. 81 and 84. Here the differentiation has become much more definite. All parts of the basidiocarp are clearly distinguishable. An annular ring of definitely compacted, downward growing filaments which make up a quite clearly defined, uniform palisade layer is present, and the loosening of the tissues below the palisade layer is much more pronounced. A continuation of this development is seen in the median and tangential longitudinal sections shown in figs. 58 and 59, and more highly magnified in figs. 82 and 85. Here the palisade layer is well developed, and a more or less complete annular rift has occurred below the palisade layer, due to the continued expansion of the more actively growing parts. The filaments making up this palisade layer are scarcely 1.5 μ in diameter, and lie closely packed together and parallel to each other.

ORIGIN AND DEVELOPMENT OF GILLS

Figs. 60–63 show a fruit body when the first signs of gill development are distinguishable. The gills originate as downward growing, radial folds of an even palisade layer. These folds extend down-

ward into the annular prelamellar chamber below the palisade region. The first folding takes place near the stipe, as can be seen in the series of tangential sections shown. The details of figs. 60 and 62 are shown in figs. 83 and 86. The young gill salients thus formed by the folding of the palisade layer, along with downward growth in radial areas, develop rapidly, and as development progresses the longest gill salients are found next to the stipe and adnate to it (figs. 64–68). The folding continues outward so that near the margin we find a uniform or level palisade layer during the period of growth. Fig. 91 is a higher magnification of the hymenium shown in fig. 67. In this series, as well as in the basidiocarp illustrated in figs. 69–73, a strongly epinastic and horizontal development is observable in the pileus, and the margin of the pileus becomes strongly incurved. As can be seen by the tangential sections, the development of the gills continues to be centrifugal, and the level palisade layer is to be found on the incurving edge of the pileus. The structure of the gills at this age can be seen in figs. 87 and 88, higher magnifications of fig. 69. The trama is composed of somewhat parallel filaments that branch sparingly until the subhymenium is reached, and then branch repeatedly to give rise to the young basidia and paraphyses. Fig. 89 shows the same condition in tangential sections in a somewhat older fruit body. Figs. 74–76 show a fruit body nearing maturity. The broad attachment of the gills to the stipe, and the general triangular shape of the gills characteristic of this genus, are also shown in the median section (fig. 74), and the attachment of the gills is also clearly shown in fig. 77, a horizontal section through the pileus of a fruit body nearing maturity. As the epinastic development of the pileus continues, the margin of the pileus becomes more and more inturned. This strong incurving of the margin of the pileus results in sections similar to the ones shown in figs. 75 and 76, where the section passes through the incurved margin of the pileus as well as through the upper portion. The stalls or pigeonholes thus formed might lead one to an erroneous idea as to the origin of the gills if their development had not been traced through the earlier stages.

The secondary gills originate in the same manner as the primary gills, but at varying distances from the stipe. Sections of some of

these may be seen in figs. 76 and 92. Here some are shown that are still in the young salient condition, and two others that have started near the point at the upper portion of the pileus at which the section was cut off and developed outward. These 2 gills are distinguishable by their narrow attachment to the upper portion of the pileus. The location of the secondary gills is clearly shown in a horizontal section through the pileus (fig. 77).

The primary gills very commonly branch as they develop. The branching is frequently dichotomous, but may be of various types, as is illustrated in fig. 77. These branches seemingly arise in much the same manner as described by SAWYER (18) for *Cortinarius pholideus*.

During the expansion of the gills the hyphae making up the trama become much enlarged and separate from each other, so that a very loose open trama results. Fig. 90 shows the structure of a gill at maturity, and a comparison with fig. 89 shows the changes taking place during the expansion of the fruit body.

CHANGES TAKING PLACE IN BLEMATOGEN DURING DEVELOPMENT

As the blematogen is first differentiated it consists of loosely interwoven filaments, which take the stain quite deeply (figs. 51–55). The cells composing it soon lose their protoplasmic content, however, the individual cells becoming inflated to 4–6 μ in diameter and the blematogen showing as a very thin layer of loosely arranged, weakly staining filaments covering pileus and stem (figs. 56–73). It becomes so delicate that it is easily destroyed even with careful handling. The boundary line between the blematogen and the surface of the pileus is never clearly defined, but at all times the one merges into the other, as described by ATKINSON (4, 7) for *Agaricus rodmani*, *A. arvensis*, and *A. comtulus*, and by ALLEN (1) for *Hypholoma*. The shedding of the blematogen is somewhat like that in *Coprinus micaceus* (8) in the manner in which the cells become constricted at the cross-walls and break off, but at no time do they arrange themselves in a definite compact palisade layer as in *C. micaceus*.

During the final expansion the blematogen becomes so thin and delicate that it breaks up into scurfy particles (fig. 74), which,

together with the expansion of the cells making up the pileus, similar to that occurring in the blematogen, give the mature pileus the furfuraceous appearance characteristic of the species. The detail of the surface of the pileus at maturity is shown in fig. 93.

ORIGIN OF MARGINAL OR PARTIAL VEIL

In the early stages of the development of the pileus the blematogen is the only distinguishable layer surrounding the fundaments of the pileus and stipe, but by the time the palisade layer has developed (fig. 81) it can be seen that there are 2 distinct regions in the portion of the veil extending between pileus and stipe. The inner region is made up largely of filaments that are continuations of the more or less parallel filaments making up the margin of the pileus that extend across and merge with those of the stipe, while the outer portion is made up of the blematogen. As the annular rift becomes increasingly larger these two regions show more clearly (fig. 83). As the fruit body expands the blematogen becomes stretched into a thinner layer, but the layers can be distinctly seen in fig. 87, where the gills are quite well developed. During the expansion of the fruit body the partial veil ruptures irregularly (figs. 74, 75), and being delicate soon disappears, so that in the mature fruit body the veil is inconspicuous if seen at all.

The development of the partial veil agrees entirely with that described by SAWYER (17) for *Pholiota*, except that the veil quite commonly ruptures near the stem instead of at the margin of the pileus. ZELLER'S (19) illustrations of *Stropharia* also show a similar partial veil, but he does not describe its structure.

Summary

PLUTEUS ADMIRABILIS

1. No entirely undifferentiated primordium of a basidiocarp was obtained. The earliest stage secured showed a differentiation into primordia of stipe, pileus, and hymenophore.

2. All parts of the young basidiocarps are covered with free ends of hyphae which lie more or less parallel to each other. The primordium of the hymenophore is distinguishable by the smaller cells composing it, with denser protoplasmic contents. It develops

at the angle of junction between pileus and stipe. This soon becomes a definite level palisade layer. It is entirely exogenous in origin.

3. There is a strong epinastic development in the margin of the pileus and it becomes so strongly incurved that the filaments on its margin intermingle with those on the surface of the stipe. This occurs while the hymenophore is still in a level palisade condition.

4. The gills originate as downward growing folds which develop centrifugally, the first folding taking place at the point where the fundament of the hymenophore was first distinguishable over the angle of stipe and pileus.

5. The secondary gills originate in the same manner as the primary gills but at varying distances from the stipe. Their development is centrifugal.

6. The primary gills during their early development are attached to the stem and only become free during the final expansion of the fruit body.

7. The cystidia are distinguishable as soon as the gill salients appear. They appear as larger cells with scanty protoplasmic content, while the smaller cells of the hymenial layer are densely filled with protoplasm.

8. The cystidia are formed terminally upon filaments similar to, but usually larger than, those that bear the smaller cells of the hymenial layer. In younger stages the filaments bearing cystidia are little if at all branched, but in older fruit bodies they become more branched. The filaments bearing basidia and paraphyses branch profusely very early in their development.

9. The surface of the pileus is covered with cells that are similar to the cystidia.

10. The trama in the young gills is composed of a few slender filaments which lie more or less parallel to each other. During expansion large elongated cells developing from the subhymenium grow inward and downward, giving a very unusual appearance to the trama. These cells probably represent internal cystidia. The cells of the original trama become much enlarged also.

11. The cells in all parts of the young basidiocarps are constantly binucleate.

TUBARIA FURFURACEA

1. The primordium of the basidiocarp consists of loosely interwoven hyphae of uniform size.

2. The development of the fruit body is endogenous. The primordium of the stipe as a conical region of small deeply staining filaments is the first to be differentiated. The primordium of the pileus originates as an outgrowth of the apical end of the elongating stipe. A well defined blematogen, consisting of the undifferentiated ground tissue, surrounds the entire young fruit body.

3. The primordium of the hymenophore appears soon after the differentiation of the primordium of the pileus. At first it is only distinguishable by its deeper staining properties, but soon the filaments in the region come to lie parallel to each other and form a definite level palisade layer.

4. The development of the primordium of the hymenophore is accompanied by a stretching apart of the filaments below it to form a definite but weak annular prelamellar cavity.

5. The gills originate as radial folds in a previously uniform palisade layer. Their development is centrifugal and they very often branch toward the margin.

6. The secondary gills develop similarly but at varying distances from the stipe.

7. The surface of the pileus is never clearly defined, but at all times merges gradually into that of the blematogen. The cells of the blematogen become inflated and easily separate from each other. For this reason it is easily destroyed.

8. The marginal or partial veil is made up of 2 layers. The outer consists of blematogen, while the inner is made up largely of filaments that are continuations of those making up the margin of the pileus, and which are also attached to the stipe. The veil ruptures irregularly at maturity and is so delicate that it soon disappears.

In conclusion, I wish to express my deep obligation to the late Professor George F. Atkinson for the use of his laboratories during the summers of 1916 and 1917, for his constant interest in my work, and for his many helpful suggestions.

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EXPLANATION OF PLATES I–V

The photomicrographs were made by the author as follows: figs. 1–28, 51–77 with a horizontal Zeiss camera; figs. 29–50, 78–93 with a Bausch and Lomb vertical camera and Zeiss lenses. Detailed explanations of figures may be found in the text.

PLATES I–III

Pluteus admirabilis

FIG. 1.—Median longitudinal section of young basidiocarp showing differentiation into primordia of stipe, pileus, and hymenophore; ×31.

FIGS. 2, 3.—Median and tangential longitudinal sections of slightly older basidiocarp, with well organized palisade layer; ×31.

FIGS. 4–8.—Successive stages in development of pileus; ×31.

FIGS. 9–11.—Median and tangential longitudinal sections of slightly older basidiocarp; ×31.

FIGS. 12–14.—Similar sections of depauperate fruit body in which development had been arrested when gill salients were forming; ×31.

FIGS. 15–18.—Median and 3 tangential longitudinal sections through basidiocarp just older than preceding.

FIGS. 19–22.—Position of these sections indicated in text fig. 2; ×31.

FIG. 23.—Median longitudinal section of basidiocarp nearing maturity; ×31.

FIG. 24.—Horizontal section through a basidiocarp about same age as shown in figs. 19–22, showing strong attachment of gills to stipe; ×31.

FIGS. 25–28.—Successive stages in development of gills; ×31.

FIG. 29.—Higher magnification of fig. 1, showing beginning of hymenophore; ×225.

FIGS. 30, 31.—Higher magnifications of basidiocarp shown in figs. 2 and 3, showing detail of palisade layer; ×225.

FIG. 32.—Detail of a part of fig. 8, showing interweaving of filaments of pileus and stipe, giving appearance of endogenous development; ×225.

FIGS. 33, 34.—Higher magnifications of sections shown in figs. 12 and 13; ×225.

FIG. 35.—Higher magnification of fig. 10; ×225.

FIG. 36.—Detail of section shown in fig. 18; ×225.

FIG. 37.—Detail of part of fig. 22; gill salients appear on incurved part of pileus; ×225.

FIG. 38.—Young gills from basidiocarp shown in fig. 20; ×225.

FIG. 39.—Part of hymenophore as seen on margin of pileus shown in fig. 24; ×225.

FIG. 40.—Portion of surface of basidiocarp shown in fig. 23; ×225.

FIG. 41.—Portion of surface of pileus of basidiocarp nearing maturity, showing character of surface of mature fruit, and loosening of tissues during expansion.

FIGS. 42–45.—Changes taking place in trama of gills during development.

FIG. 42.—Part of gill from fig. 25; ×225.

FIG. 43.—Part of gill from fig. 26; ×225.

FIGS. 44, 45.—Parts of gills from figs. 27 and 28; ×225.

FIG. 46.—Some of hymenium of basidiocarp shown in fig. 28; ×225.

FIGS. 47, 47*a*.—Parts of gills from basidiocarp shown in figs. 19–22, 37, 38; ×585.

FIG. 48.—Similar section to those of fig. 47 from slightly older fruit body (see text fig. 5); ×585.

FIG. 49.—Single basidium in detail; ×936.

FIG. 50.—Free-hand section of gill of *Pluteus seticeps* Atk. MSS; × 225.

PLATES IV, V

Tubaria furfuracea

FIG. 51.—Median longitudinal section of undifferentiated primordium of basidiocarp; ×33.

FIG. 52.—Median longitudinal section of early stage in differentiation of basidiocarp showing primordia of stipe, pileus, and blematogen; ×33.

FIG. 53.—Median longitudinal section of basidiocarp intermediate in development between figs. 51 and 52; ×33.

FIGS. 54, 55.—Median and tangential longitudinal sections of slightly older basidiocarp showing primordium of hymenophore as a deeper staining region on under surface of pileus; ×33.

FIGS. 56, 57.—Median and tangential longitudinal sections of basidiocarp just older than fig. 54; ×33.

FIGS. 58, 59.—Median and tangential longitudinal sections of basidiocarp with well developed palisade layer and more definite rift below; ×33.

FIGS. 60–63.—Median and tangential longitudinal sections of basidiocarp, showing first traces of gill salients; ×33.

FIGS. 64–68.—Median and tangential longitudinal sections of young basidiocarp showing centrifugal development of gills; ×33.

FIGS. 69–73.—Median and tangential longitudinal sections of older basidiocarp showing centrifugal development, attachment of gills, and breaking up of blematogen layer into flaky particles over pileus; ×33.

FIGS. 74–76.—Median and tangential longitudinal sections of basidiocarp nearing maturity; secondary gill development shown in figs. 75 and 76; ×33.

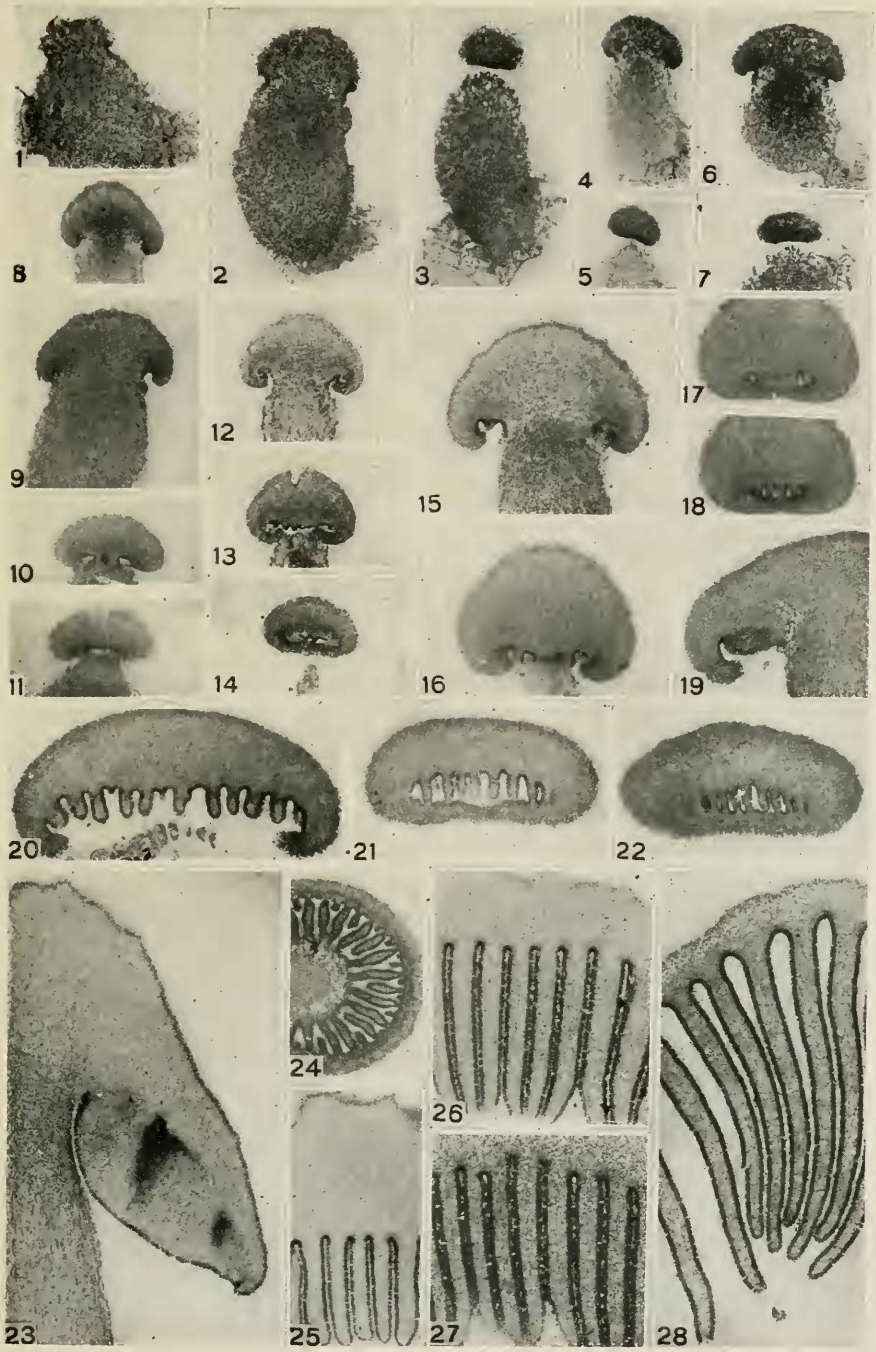
FIG. 77.—Transverse section of basidiocarp showing arrangement and branching of primary and secondary gills; ×12.

FIG. 78.—Upper part of section shown in fig. 51; ×200.

FIG. 79.—Detail of upper portion of basidiocarp shown in fig. 52; ×200.

FIG. 80.—Detail of upper portion of basidiocarp shown in fig. 54; ×200.

FIG. 81.—Upper portion of section shown in fig. 56, showing structure of hymenophore and veil; ×200.



WALKER on PLUTEUS and TUBARIA